

AN EXPERIMENTAL STUDY OF PREDATION ON ARTIFICIAL NESTS IN ROADSIDES ADJACENT TO AGRICULTURAL HABITATS IN IOWA

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ABSTRACT.—We quantified predation on artificial nests in Iowa roadsides and examined the relationships between nest predation and characteristics of roadsides. Transects consisting of 10 nests (five in the foreslope and five in the backslope) were set up in 136 roadsides in six watersheds in south-central Iowa. Most roadsides had herbaceous vegetation with fences (67%); fewer were wooded (18%) or had herbaceous vegetation without fences (15%). Most roads were gravel (80%), and most roadsides were adjacent to row crops (63%). Average total nest predation per transect was 23% (SE = 2), ranging from 0 to 100%. Nest predation was categorized into one of three outcomes: disappearance of eggs without disturbance to the nest bowl (39%), disappearance of eggs with disturbance to the nest bowl (17%), and broken or crushed egg shell fragments in or near the nest bowl (44%). Wooded roadsides and herbaceous roadsides with fences had significantly greater nest predation than herbaceous roadsides without fences for disappearance of eggs without disturbance to the nest bowl. Backslopes had significantly greater nest predation than foreslopes for all outcome categories except the disappearance of eggs with disturbance to the nest bowl. Wooded roadsides and herbaceous roadsides with fences along the backslope may provide cover and travel corridors for mammalian predators or elevated perches for avian predators. *Received 22 Aug. 1996, accepted 27 Feb 1997.*

Nest predation is an important cause of mortality for many bird species (Ricklefs 1969, Martin 1988), especially in grassland ecosystems where predators have responded positively to human disturbance and landscape fragmentation (Warner 1994). For example, more than half of the Dickcissel (*Spiza americana*) nests in grassland and old field habitats in Kansas (Zimmerman 1984) and half of the ground nests of a southern Maine grassland bird community suffered nest predation (Vickery et al. 1992). Grasslands have been fragmented and disturbed by agriculture over much of North America, contributing to the decline of populations of grassland birds (Askins 1994, Herkert 1994) and creating a landscape mosaic of large blocks of cropland, small patches of remnant prairie or other grassed habitats, and an interconnected network of strip-cover habitats (Warner 1994). Where agriculture has become intense, grassed habitat persists primarily as strip cover such as roadsides, grassed waterways, and fence-rows.

Roadside vegetation may be of critical importance to ground-nesting birds in agricultural landscapes by providing relatively undisturbed habitat

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for nesting (Best 1986, Camp and Best 1993, Warner 1994). Roadsides have been shown to have greater avian abundance and species richness than adjacent croplands (Camp and Best 1993, Best et al. 1995). However, evaluations of habitat quality on the basis of abundance data alone can be misleading, because the correlation between population density and reproductive success is often poor (Van Horne 1983, Vickery et al. 1992). Strip-cover habitats, such as roadsides, can serve as corridors or travel lanes for predators, interconnecting non-linear, block-cover habitats (e.g., grasslands and woodlands), which may serve as potential sources of predators (Rodenhouse and Best 1983, Moller 1989). Roadsides also may prove to be "ecological traps," which attract high densities of nesting birds but lead to low nest success because of increased nest predation (Gates and Gysel 1978, Best 1986, Warner 1994).

Compared with other roadside studies (Snyder 1974, Warner and Josselyn 1986, Warner et al. 1987, Camp and Best 1994), our study increased the sample size, broadened the geographic scope by using six different watersheds, used artificial nests instead of natural nests for more rigorous experimental control, and compared different types of roadsides adjacent to different habitats. The objectives of our study were to quantify levels and assess patterns of nest predation in Iowa roadsides, to identify potential nest predators in Iowa roadsides, and to examine the relationships between nest predation and characteristics of roadsides and adjacent habitats.

METHODS

Study areas.—We selected six Iowa watersheds for study in 1994 which represented a range of agricultural landscapes from mostly row crops to more forage/pasture, Conservation Reserve Program (CRP) land, and woodland. The topography ranged from mainly flat to steeply rolling (Prior 1991). The Bear Creek watershed in Hamilton and Story counties and the Walnut Creek (Story) watershed in Story and Boone counties are located in the relatively flat Des Moines lobe created by the Wisconsin glacier. The Buck Creek watershed in Poweshiek County, the Walnut Creek (Jasper) watershed in Jasper County, the Seven Mile Creek watershed in Cass County, and the Three Mile Creek watershed in Adair and Union counties are located in the rolling Southern Iowa Drift Plain.

Differences in weather conditions among watersheds and between experimental periods (see below) could have affected nest predation, so for each watershed, the mean daily maximum temperature and total rainfall during each experimental period were quantified by using data reported from the nearest weather station or, if equidistant, the means from the two nearest stations. Temperature and rainfall data were obtained from the Iowa Dept. of Agriculture and Land Stewardship (1994).

Nest predation.—Artificial nests were set up in linear transects in roadsides, with 16 to 28 transects per watershed depending on watershed size ($N = 136$ replicates). Iowa roads usually demarcate one-mile² (1.7 km²) sections, and we took advantage of this grid system to randomly locate transects within the watersheds. Only one transect was placed within each section studied; the roadside selected was randomly chosen from among the four sides of

the section. A 200-m-long buffer was maintained on each end of the roadside to minimize the effect of intersecting roads on the transect. The transect was randomly positioned between the end buffers. Transects in adjacent sections were not located along the same 1-mile segment of road to maintain the independence of each transect. Finally, transects were positioned such that they did not cross drainages, watercourses, or roadways that might have artificially divided the transect into different segments, potentially preventing predators from responding to each transect as a unit.

Each transect was 180 m long and contained 10 artificial nests at 20-m intervals along the transect. Locations of the artificial nests within the transect were alternated between a position 2 m from the road edge (foreslope) and a position next to the adjacent habitat (backslope), which was often separated from the roadside by a fence. Nests on the same side of the roadside were separated by 40 m to reduce the likelihood that a predator would find an adjacent nest after discovering an initial nest. At each nest site, vegetation and litter were scraped from a small area of the soil surface with a garden trowel. A white plastic tag (2 × 7 cm) was secured to the ground at the center of the scrape with a 16-penny nail. This marker, concealed by the nest bowl and eggs, validated the location of a nest if the nest and its contents were removed or disturbed by predators or weather. A nest bowl was fashioned from herbaceous plant material available near the nest site, and two Japanese Quail (*Coturnix coturnix*) eggs were placed in the nest bowl. The quail eggs were obtained from a game farm in late May. Eggs were refrigerated until the day they were set out. The eggs and nest materials were handled with rubber gloves, and field technicians wore rubber boots to reduce human scent. Plastic flagging, placed across the roadside opposite each nest (at least 5 m away), was used to mark nest locations without attracting predators. Care was taken to avoid disturbing the vegetation near nest sites.

Artificial nests were set up in two consecutive two-week periods from 31 May through 28 June, the main breeding season for common farmland birds in Iowa (Best 1986). To minimize bias, half of the transects for each watershed were set up in each experimental period and distributed uniformly from the upper to lower portions of the watershed. For each transect, the artificial nests remained in place for seven days and were checked only at the end of that period, thus minimizing the effects of human disturbance. We recorded the condition of the eggs and the nest bowl. If at least one egg was broken or removed, the nest fate was assigned to predation. A few nests were disturbed by weather or mowing and were not included in the nest outcome tabulation. The number of eggs lost per nest and adjacent nest losses within a transect were documented for each nest site and transect. For each transect the proportion of nests lost to predation was calculated for the foreslope, backslope, and the total transect.

Sightings, tracks, or scat of potential predators were noted whenever observed. No special means, such as hair catchers or camera setups, were used to identify predators in our study. Even though the attribution of nest predation events to specific predators is problematical, because of overlap in the egg-handling behavior of various predator species (Rearden 1951, Einarsen 1956, Trevor et al. 1991), we categorized nest predation on the basis of the physical evidence left at the nest site. The three outcome categories were: disappearance of eggs without disturbance to the nest bowl, disappearance of eggs with disturbance to the nest bowl, and broken or crushed egg shell fragments near the nest site, whether the nest was disturbed or not.

Roadside characterization.—Our study examined several roadside characteristics and their relationships to nest predation. Specifically, we asked if nest predation in roadsides was related to roadside habitat, road type, adjacent habitat, position within the roadside, roadside width, roadside depth, and height differential between the roadside foreslope and backslope. The habitat of each roadside transect was characterized on the basis of the extent

of woody cover and the presence or absence of a fence along the backslope. Categories included: herbaceous (<5% woody cover) without a fence, herbaceous with a fence, and wooded (>5% woody cover). The road type adjacent to each transect was either gravel or paved, and the habitat adjacent to each transect backslope was designated as either row crop or non-row crop (i.e., other block-cover habitats). If both habitat types were adjacent to the transect, the predominant one was used. The width, maximum depth, and height differential of each roadside were measured at the two points 60 m internally from each end of the transect; the two values were then averaged.

Statistical analysis.—Nest predation data (i.e., the proportion of nests lost per transect) for each outcome category were adjusted using the arcsine transformation to better approximate a normal distribution and stabilize the variance (Scheffe 1959, Zar 1984). Each outcome category was examined separately in the analyses described below. Statistical significance was set at $P < 0.05$. All analyses were performed with the Statistical Analysis Software 6.09 (SAS Institute Inc. 1994).

We looked for differences in weather conditions and nest predation among watersheds and between experimental periods to determine if the data could be pooled. The two weather variables and each nest predation outcome category were examined by using two-factor analyses of variance (ANOVA) (Zar 1984). If any ANOVA (including those described below) was statistically significant for a factor, a Student-Newman-Keul's (SNK) multiple range test was used to determine which classes of the factor were significantly different (Steel and Torrie 1980).

Nest predation was evaluated relative to roadside characteristics; both categorical and continuous variables were used. The categorical variables, which included roadside habitat, road type, adjacent habitat, and position in the roadside, were analyzed by using four-factor ANOVA (Zar 1984). The within transect error term was used in the F -test for position in roadside and the among transect error term for roadside habitat, road type, and adjacent habitat. The continuous variables, which included roadside depth, width, and height differential, were analyzed by using multiple regression (Draper and Smith 1981).

RESULTS AND DISCUSSION

The mean width of roadsides was 8.2 m (SE = 0.3), the mean depth was 1.3 m (0.07), and the mean height differential between the foreslope and backslope was 0.7 m (0.06); backslopes generally were lower than foreslopes. Most roadsides had herbaceous vegetation with fences (67%); fewer were wooded (18%) or had herbaceous vegetation without fences (15%). Most roads were gravel (80%), and most roadside transects were adjacent to row crops (63%).

The average total nest predation across all roadside transects was 23% (SE = 2). The disappearance of eggs without disturbance to the nest bowl comprised 39% of the total nest predation, disappearance of eggs with disturbance to the nest bowl 17%, and predation with egg shell fragments remaining in or near the nest bowl 44%. The distribution of the proportion of nests lost to predation per transect was skewed toward the low end of the scale for each outcome category (Fig. 1). Most transects had either no nests or only one nest lost to predation. Three transects, however, had at least 80% nest loss, and one suffered complete nest loss. The average

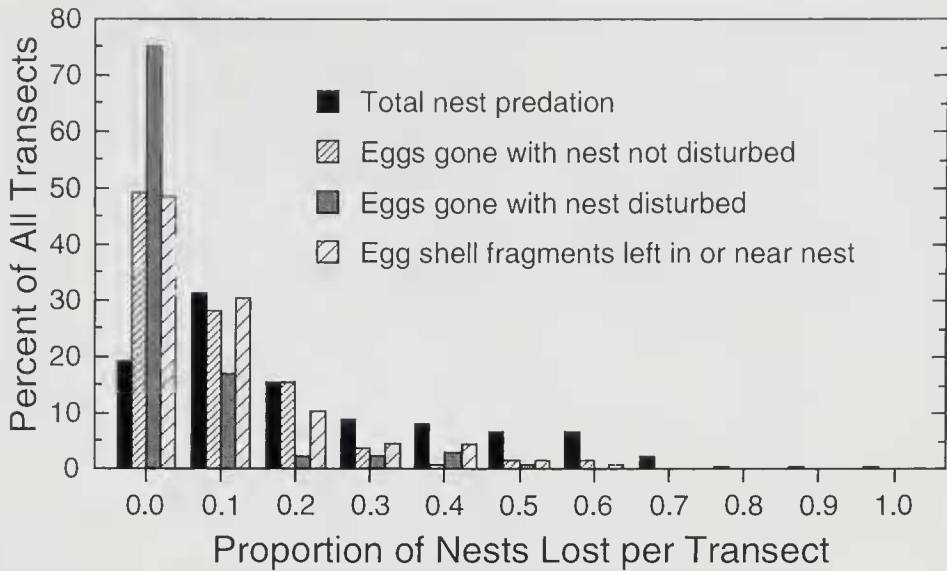


FIG. 1. The distribution of the proportion of nests lost per transect for each nest predation outcome category ($N = 136$).

total nest predation within watersheds ranged from a low of 14% in Walnut Creek (Story) to a high of 32% in Three Mile Creek (Table 1). The disappearance of eggs without disturbance to the nest bowl ranged from 5–15% among the six watersheds, disappearance of eggs with disturbance to the nest bowl 1–6%, and predation with egg shell fragments remaining in or near the nest bowl 4–13%.

Mean maximum daily temperature and total rainfall were not significantly different between experimental periods or among watersheds. The mean daily maximum temperature was 28°C, and the mean total rainfall was 10 cm over the entire study period. The proportion of nests lost to predation was not significantly different between experimental periods for any outcome category (Table 2). Watersheds did differ significantly in the disappearance of eggs without disturbance to the nest bowl; Bear Creek (greatest predation) and Walnut Creek (Story) (least) were significantly different from each other but not from the other four watersheds (SNK multiple range test). Given the similarity in weather conditions among watersheds and between experimental periods and the fact that only one nest predation outcome category differed among watersheds, we pooled the data in further analyses.

Most studies of nest predation in roadsides have focused on natural nests, primarily those of the Ring-necked Pheasant (*Phasianus colchicus*); nest predation in those studies ranged from 39 to 55% (Snyder 1974, Warner and Joselyn 1986, Warner et al. 1987, Camp and Best 1994). Our study had a lower average total nest predation of 23%, but showed a broad range among transects (0–100%). Our artificial nests had lower

TABLE 1
 MEAN PROPORTION (STANDARD ERROR) OF NESTS LOST TO PREDATION PER TRANSECT IN FORESLOPES AND BACKSLOPES OF ROADSIDES, FOR EACH
 NEST PREDATION OUTCOME CATEGORY, AND FOR TOTAL NEST PREDATION

Watershed	No. of transects	Nest predation outcome categories ^a					Total
		Foreslope	Backslope	Eggs gone with nest not disturbed	Eggs gone with nest disturbed	Egg shell fragments	
Bear Creek	20	0.15 (0.04)	0.34 (0.08)	0.05 (0.02)	0.06 (0.02)	0.13 (0.04)	0.24 (0.05)
Buck Creek	28	0.08 (0.02)	0.29 (0.06)	0.10 (0.02)	0.05 (0.02)	0.04 (0.01)	0.20 (0.04)
Seven Mile Creek	28	0.21 (0.05)	0.31 (0.05)	0.09 (0.02)	0.04 (0.02)	0.13 (0.03)	0.26 (0.04)
Three Mile Creek	24	0.28 (0.06)	0.34 (0.06)	0.15 (0.03)	0.05 (0.02)	0.11 (0.02)	0.32 (0.05)
Walnut Creek (Story)	16	0.10 (0.04)	0.18 (0.07)	0.09 (0.02)	0.01 (0.01)	0.09 (0.04)	0.14 (0.04)
Walnut Creek (Jasper)	20	0.14 (0.05)	0.28 (0.07)	0.09 (0.03)	0.04 (0.02)	0.10 (0.03)	0.21 (0.06)
All watersheds	136	0.16 (0.02)	0.30 (0.03)	0.09 (0.01)	0.04 (0.01)	0.10 (0.01)	0.23 (0.02)

^a Potential nest predators listed in order of likelihood: eggs gone with nest not disturbed—raccoon, red fox, corvids, and snakes; eggs gone with nest disturbed—raccoon, red fox, and coyote; and shell fragments remaining near nest—striped skunk, coyote, thirteen-lined ground squirrel, and mink. References for characteristics to identify predators: Sooter 1946, Rearden 1951, Einarsen 1956, and Trevor et al. 1991.

TABLE 2
RESULTS FROM ANALYSES OF VARIANCE (N = 136)

ANOVA factor	df	F-statistic ^a			
		Eggs gone with nest not disturbed	Eggs gone with nest disturbed	Egg shell fragments	Total
Experimental period	1	2.29	0.89	0.26	1.29
Watershed	5	2.32*	0.91	1.53	1.89
Experimental period × watershed	5	0.93	1.68	2.45*	0.69
Error	124				
Total	136				
Roadside habitat	2	3.69*	1.74	0.57	2.73
Road type	1	1.23	0.25	1.79	0.02
Adjacent habitat	1	0.92	0.49	0.91	0.15
Position in roadside	1	13.88**	0.98	8.51**	20.60**
Error (among transects) ^b	131				
Error (within transects) ^c	131				
Total	272				

* = $P < 0.05$ and ** = $P < 0.01$.

^b Error term used for roadside habitat, road type, and adjacent habitat (among transect factors).

^c Error term used for position within roadside (within transect factor).

predation than natural nests for several possible reasons. First, our artificial nests probably had less scent than natural nests. The natural scent from incubating females was not present, and the scent from Japanese Quail females on the eggs undoubtedly had diminished in the several-week interval from laying to the setup in roadsides. This lack of scent would be most important for nocturnal mammalian predators that rely primarily on olfaction to discover nests (Whelan et al. 1994). Second, artificial nests lack the activities of adults and nestlings, such as foraging bouts and vocalizations. Avian predators such as American Crows (*Corvus brachyrhynchos*) may use adult or nestling activity as one of the cues for discovering concealed natural nests (Einarsen 1956). If true, then avian predation on artificial nests should be less than what might be expected for natural nests. In general, most predation on ground nests is mammalian rather than avian (Mankin and Warner 1992, Seitz and Zegers 1993). It is noteworthy that nest predation in our study was lower than that for two others using artificial nests in roadsides (62 and 34%; Storaas 1988, Mankin and Warner 1992). Perhaps predator densities were lower in our study, but we could not verify this.

We identified several potential nest predator species, including the raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), striped skunk (*Mephitis*

mephitis), and coyote (*Canis latrans*), from tracks left in muddy or dusty ground near transects. Canid scat also was found near some transects. Other potential nest predator species observed in the watersheds, although not necessarily near transects, included the badger (*Taxidea taxa*), thirteen-lined ground squirrel (*Citellus tridecemlineatus*), mink (*Mustela vison*), American Crow, Common Grackle (*Quiscalus quiscula*), Blue Jay (*Cyanocitta cristata*), and bullsnake (*Pituophis melanoleucus sayi*).

The removal of eggs from nests with no egg shell fragments remaining near the nest bowl (55% of the total nest predation) suggests that the predators either consumed the eggs whole or carried the eggs some distance from the nest before they were consumed. Only certain nest predators are capable of these behaviors (Rearden 1951, Einarsen 1956, Best 1978, Trevor et al. 1991). Snakes are known to swallow eggs, but we have found no documentation that mammals do. Raccoons have paws capable of handling eggs and red foxes have narrow snouts that can reach into nest bowls; both are known to carry eggs away from nests. American Crows also can carry small eggs in their bills. Raccoons and red foxes are more likely to disturb the nest bowl when removing eggs than either corvids or snakes (Rearden 1951, Einarsen 1956, Trevor et al. 1991).

Broken egg shells or fragments remaining in or near the nest bowl (44% of the total nest predation) were likely attributable to either striped skunks or coyotes. Skunks cannot carry eggs and almost always leave shell fragments in or near the nest after orally extracting the contents and spitting out the shells (Rearden 1951, Einarsen 1956); coyotes break open eggs and lap up the contents (Sooter 1946). Raccoons may leave egg shell fragments but usually not at the nest site (Rearden 1951). Small mammals potentially could leave shell fragments, but studies suggest that Japanese Quail eggs are too large and(or) the shells are too thick to be readily handled by small mammals (DeGraaf and Maier 1996).

Of 307 nests lost to predation, 23% had only one egg taken, suggesting that a predator removed an egg and consumed it at another location but did not return to the nest. As noted above, several potential predators remove eggs from nests before consumption. Forty-six transects (34%) had two or more adjacent nests lost to predation, suggesting that predators such as raccoons searched for food in a directional manner by moving from one end of a transect to the other. Predation on adjacent nests was significantly more frequent in backslopes than in foreslopes (48 vs. 27% of transects with predation on that slope of the roadside; $\chi^2 = 4.54$, $df = 1$, $P < 0.05$).

Small-scale roadside characteristics influenced nest predation (Table 2). The disappearance of eggs without disturbance to the nest bowl was significantly greater in wooded roadsides and herbaceous roadsides with

fences than in herbaceous roadsides without fences (13 and 9 vs 3%). Backslopes had significantly greater nest predation than foreslopes for three outcome categories: the disappearance of eggs without disturbance to the nest bowl (12 vs 6%), predation with egg shell fragments remaining in or near the nest bowl (12 vs 7%), and total nest predation (30 vs 16%). Road type and adjacent habitat did not significantly affect nest predation. None of the four-factor ANOVA's showed significant interactions. The multiple regression analyses did not detect any significant relationships between nest predation and the continuous variables (roadside depth, width, and height differential).

Wooded roadsides and herbaceous roadsides with fences along the backslope may provide cover for mammalian predators and elevated perches for avian predators. Some predators such as raccoons and American Crows have affinities for wooded habitats and may be more likely to use wooded roadsides for foraging (Glueck *et al.* 1988, Andren 1992). The increased vertical structure and woodiness along the fences that separate the backslopes of roadsides from adjacent habitats may facilitate predator movements, which probably use the space between fences and row-crop fields as travel corridors (Rodenhouse *et al.* 1995). Backslopes had a greater level of adjacent-nest predation than did foreslopes, indicating either that more predators were moving along the backslopes or individual predators focused their search effort in backslopes. Foreslopes, which are more likely to be mowed (12% of foreslopes and 0% of backslopes in our study), may be avoided because predators are wary of openness and(or) human traffic on adjacent roads. Natural bird nests also are more abundant in backslopes of roadsides and the associated fencelines than in foreslopes (Camp and Best 1994), which may help explain why nest predation was more common in backslopes. If predators respond to greater nest density with increased search effort, then proportionally more nests would be located and destroyed by predators in backslopes.

The implementation of our study revealed potential limitations in its design. Although artificial nests have some advantages over natural nests in quantifying and assessing the patterns of nest predation, they also have some inherent drawbacks because artificial nests may not adequately represent natural nests (Major and Kendal 1996). One potential limitation of our study was that the inter-nest distance of 40 m may have been too short. A predator could have anticipated the next nest after discovering the initial nest(s), but we found little supporting evidence. Rarely were more than two consecutive nests disturbed. Another potential limitation was that the nest positions may have been too regularly spaced. Predators are probably better at locating nests in regular than in random patterns. Thus, our study might have been improved had we randomized the inter-

nest distances. We also placed nests in consistent positions within the roadside profile (alternating between foreslope and backslope), producing two linear groups of nests in each transect. These groups were parallel to potential travel corridors, which could have increased the likelihood of predators finding nests, especially in the backslopes. Randomizing the position of nests along the roadside cross section could have reduced this possibility. We have no direct evidence, however, that any of the above-mentioned potential limitations actually affected our results.

Our study emphasized small-scale habitat effects, but the surrounding landscape mosaic also may affect nest predation (e.g., Nour et al. 1993, Robinson et al. 1995, Yahner and Mahan 1996). Analyses at the landscape scale could provide additional insights into nest predation in Iowa roadsides.

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